

LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF
NEASPILOTA PUBESCENS FREIDBERG AND MATHIS (DIPTERA:
TEPHRITIDAE) ON *LESSINGIA FILAGINIFOLIA* (HOOKER AND ARNOTT)
M. A. LANE (ASTERACEAE) IN SOUTHERN CALIFORNIA

RICHARD D. GOEDEN

Department of Entomology, University of California, Riverside, CA 92521, U.S.A.
(e-mail: rgoeden@ucr.ucr.edu)

Abstract.—*Neaspilota pubescens* Freidberg and Mathis is a univoltine, monophagous fruit fly (Diptera: Tephritidae) developing solely in the flower heads of *Lessingia filaginifolia* (Hooker and Arnott) M. A. Lane (Asteraceae) belonging to the subtribe Solidaginiinae of the tribe Astereae in southern California. The egg, second- and third-instar larvae, and puparium are described and figured. The anterior thoracic spiracle of the second instar has five papillae, reduced to two papillae in the third instar. The second instar has seven oral ridges and the third instar eight oral ridges, which, except for the most ventral, eight oral ridge in the latter instar, are ventrally toothed. The arrangement of these oral ridges in a vertical series lateral to the oral cavity is a distinguishing generic character. The larvae feed mainly on the ovules and soft achenes as first and second instars; however, as third instars, they may extend their feeding into the receptacle and supplement their diet with sap. The nonfeeding prepuparium overwinters in a protective cell that occupies much of the excavated flower head and is formed of ovule-, achene-, chaff-, pappus-, and corolla-fragments impregnated with excess sap and liquid feces that harden when dry. A few prepuparia pupate and emerge from their cells in the late summer and probably overwinter as adults, but most pupariate during the next year in late spring, and emerge as adults that aggregate on preblossom host plants to mate and subsequently oviposit. *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared as a solitary, larval-pupal endoparasitoid from a puparium of *N. pubescens*.

Key Words: Insecta, *Neaspilota*, *Lessingia*, Asteraceae, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, monophagy, seed predation, parasitoid

Revision of the genus *Neaspilota* (Diptera: Tephritidae) by Freidberg and Mathis (1986) facilitated determination of specimens reared from California Asteraceae (Goeden 1989) and stimulated several life-history studies, including those on *N. viridescens* Quisenberry (Goeden and Headrick 1992), *N. wilsoni* Blanc and Foote (Goeden and Headrick 1999), *N. signifera* (Coquillett) (Goeden 2000a), *N. aenigma* Freidberg and Mathis (Goeden 2000b), and *N. appendiculata* Freidberg and Mathis (Goeden 2000c). This paper describes some imma-

ture stages and the life history of a sixth species from California, *N. pubescens* Freidberg and Mathis.

MATERIALS AND METHODS

The present study was based in large part on dissections of flower heads of *Lessingia filaginifolia* (Hooker and Arnott) M. A. Lane (Asteraceae) collected during 1990–1997 mainly from the following two locations in the South and North Sections, respectively, of the San Bernardino National

Forest: Bautista Canyon at 1,100 m elevation, Riverside Co. and North of South Fork Campground at 1,550 m, SW San Bernardino Co. One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Eight second- and 12 third-instar larvae and five puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional prepuparia and puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied and photographed with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated prepuparia and puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for studies of longevity and sexual maturation in the insectary of the Department of Entomology, University of California, Riverside, at $25 \pm 1^\circ\text{C}$, and 14/10 (L/D) photoperiod. Two pairs of virgin males and females obtained from emergence cages also were held in each of six, separate, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden (2000a, b, c), Goeden et al. (1998), Goeden and Headrick (1992, 1999), Goeden and Teerink (1997; 1998; 1999a, b), Teerink and Goeden (1999), and our earlier works cited therein. Means \pm SE are used throughout this paper. Voucher specimens of *N. pubescens* immature stages, adults, and parasitoids reside in my research collections.

RESULTS AND DISCUSSION

Taxonomy

Adult.—*Neaspilota pubescens* was described by Freidberg and Mathis (1986: 55–57), who pictured the unpatterned wing, along with drawings (p. 56) of the lateral aspect of the head; male right foretarsus, epandrium, distiphallus, epandrium and cerci, aculeus and its apex enlarged, and spermatheca.

Immature stages.—The first-instar larva remains undescribed, but the egg, second- and third-instar larvae and puparium are described below, as the only stages available at this writing.

Egg: Only three intact eggs were found and measured *in situ* within separate, immature, preblossom flower heads. These eggs were white, opaque, smooth, elongate-ellipsoidal, and averaged 0.71 ± 0.03 (range, 0.64–0.74) mm long and 0.18 ± 0.003 (range, 0.17–0.18) mm wide, tapered and smoothly rounded at both ends. As no eggs were examined by scanning electron microscopy, the egg of *N. pubescens* could only be generally compared with the eggs of *N. viridescens*, *N. wilsoni*, and *N. appendiculata*, which were described in detail by Goeden and Headrick (1992, 1999) and Goeden (2000c).

Second instar: White, elongate-cylindrical, rounded anteriorly, truncated dorsoposteriorly (Fig. 1A), body segments well-de-

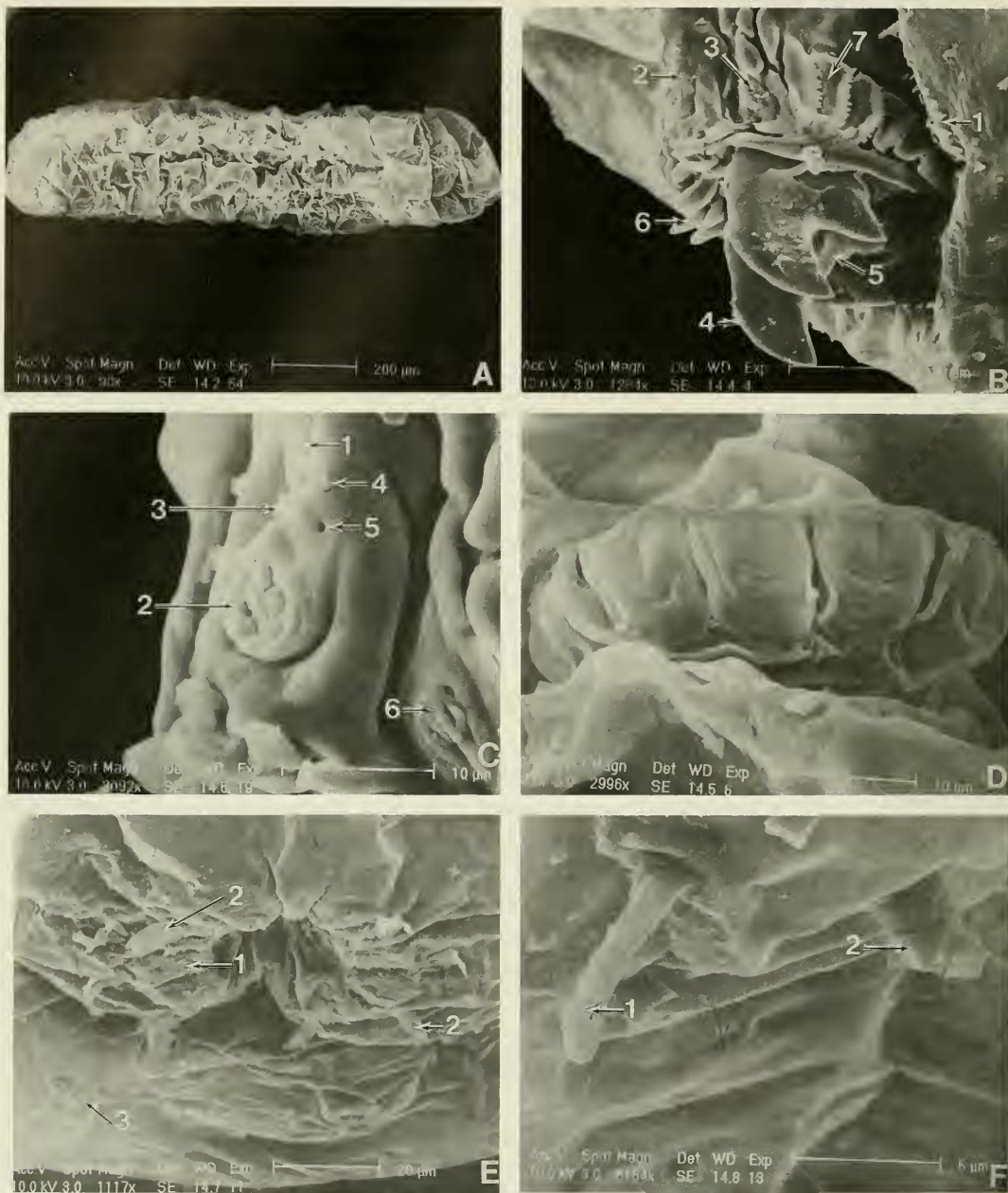


Fig. 1. Second instar of *Neaspilota pubescens*: (A) habitus, anterior to left; (B) gnatophcephon, ventrolateral view, 1-minute acanthae, 2-anterior sensory lobe, 3-stomal sense organ, 4-mouthhook, 5-median oral lobe, 6-integumental petal, 7-oral ridge; (C) anterior sensory lobe, 1-dorsal sensory organ, 2-terminal sensory organ, 3-lateral sensory organ, 4-supralateral sensory organ, 5-pit sensory organ, 6-stomal sense organ; (D) anterior thoracic spiracle; (E) caudal segment, 1-rima, 2-interspiracular process, 3-intermediate sensory complex; (F) intermediate sensory complex, 1-stelex sensillum, 2-medusoid sensillum.

finned, circumscribed anteriorly with few minute acanthae (Figs. 1B-1); dorsal sensory organ well-defined, dome-shaped (Fig. 1C-1); anterior sensory lobe (Fig. 1B-2, C) with terminal sensory organ (Fig. 1C-2), lateral sensory organ (Fig. 1C-3), supralateral sensory organ (Fig. 1C-4), and pit sensory organ (Fig. 1C-5); stomal sense organ (Figs. 1B-3, C-6) ventrolaterad of anterior sensory lobe; mouthhook bidentate (Fig. 1B-4); median oral lobe (Fig. 1B-5), flabelliform, laterally compressed (not shown); about six papilliform, integumental petals dorsal to each mouthhook (Fig. 1B-6); seven oral ridges toothed ventrally, in vertical series lateral to oral cavity (Fig. 1B-7); prothorax, at least, circumscribed anteriorly by posteriorly-directed, minute acanthae (Fig. 1B-1); anterior thoracic spiracle with five, cuboidal papillae (Fig. 1D); lateral spiracular complexes not seen; caudal segment with two stelex sensilla (not shown) dorsolaterad and ventrolaterad of posterior spiracular plate (Fig. 1E); posterior spiracular plate bears three ovoid rimae (Fig. 1E-1), ca. 0.015 mm long, and four interspiracular processes (Fig. 1E-2), each with one to four, simple or forked branches, longest measuring 0.01 mm; intermediate sensory complex (Figs. 1E-3, F) with a stelex sensillum (Fig. 1F-1) and a medusoid sensillum (Fig. 1F-2).

The habitus of the second instar of *N. pubescens* (Fig. 1A) is more like *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c) than the barrel-shaped second instar of *N. viridescens* (Goeden and Headrick 1992). The dorsal sensory organ of *N. pubescens* is well defined in the second instar (Fig. 1C-1), as with *N. signifera* (Goeden 2000a) and *N. appendiculata* (Goeden 2000c), but is not well defined in *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), and *N. aenigma* (Goeden 2000b). The integumental petals of the second instars of all six species are papilliform and six in number

in *N. pubescens* (Fig. 1B-6), like *N. viridescens* (Goeden and Headrick 1992), but number four in *N. signifera* (Goeden 2000a), seven in *N. wilsoni* (Goeden and Headrick 1999) and *N. appendiculata* (Goeden 2000c) and eight in *N. aenigma* (Goeden 2000b). In the first instars of all six congeners examined to date, though not available in the present study, the integumental petals are broad, flattened, and paired (Goeden and Headrick 1992, 1999; Goeden 1999a, b). An apparent difference in *N. pubescens* is the five papillae on the anterior spiracle of the second instar (Fig. 1D), compared to eight in *N. appendiculata* (Goeden 2000c), and three to four papillae in second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b). Finally, the interspiracular processes of *N. pubescens* each bear one to four branches like *N. aenigma* (Fig. 1E-2, Goeden 2000b), not two to four branches like *N. signifera* (Goeden 2000a), nor five to nine branches like those of *N. viridescens* (Goeden and Headrick 1992), nor two to six branches like those of *N. wilsoni* (Goeden and Headrick 1999), nor four branches like those of *N. appendiculata* (Goeden 2000c). However, it is recognized that most specimens of *N. pubescens* with branch numbers at the high end of the range will not differ from most other *Neaspilota* in this character.

Third instar: Pale yellow, ellipsoidal, with posterior spiracular plate dark brown to black, tapering anteriorly; posterior spiracular plate on caudal segment flattened and upturned dorsally ca. 60° (Fig. 2A), minute acanthae circumscribe anterior fifth of thoracic and anterior abdominal segments, but more common posteriorly (Fig. 2B-1); gnathocephalon conical (Fig. 2B); dorsal sensory organ an elliptical, flat, poorly defined pad (Fig. 2C-1) punctured centrally and peripherally by pore sensilla (Fig. 2C-2); anterior sensory lobe (Fig. 2C) bears terminal sensory organ (Fig. 2C-3), lateral sensory organ (Fig. 2C-4), supralateral sen-

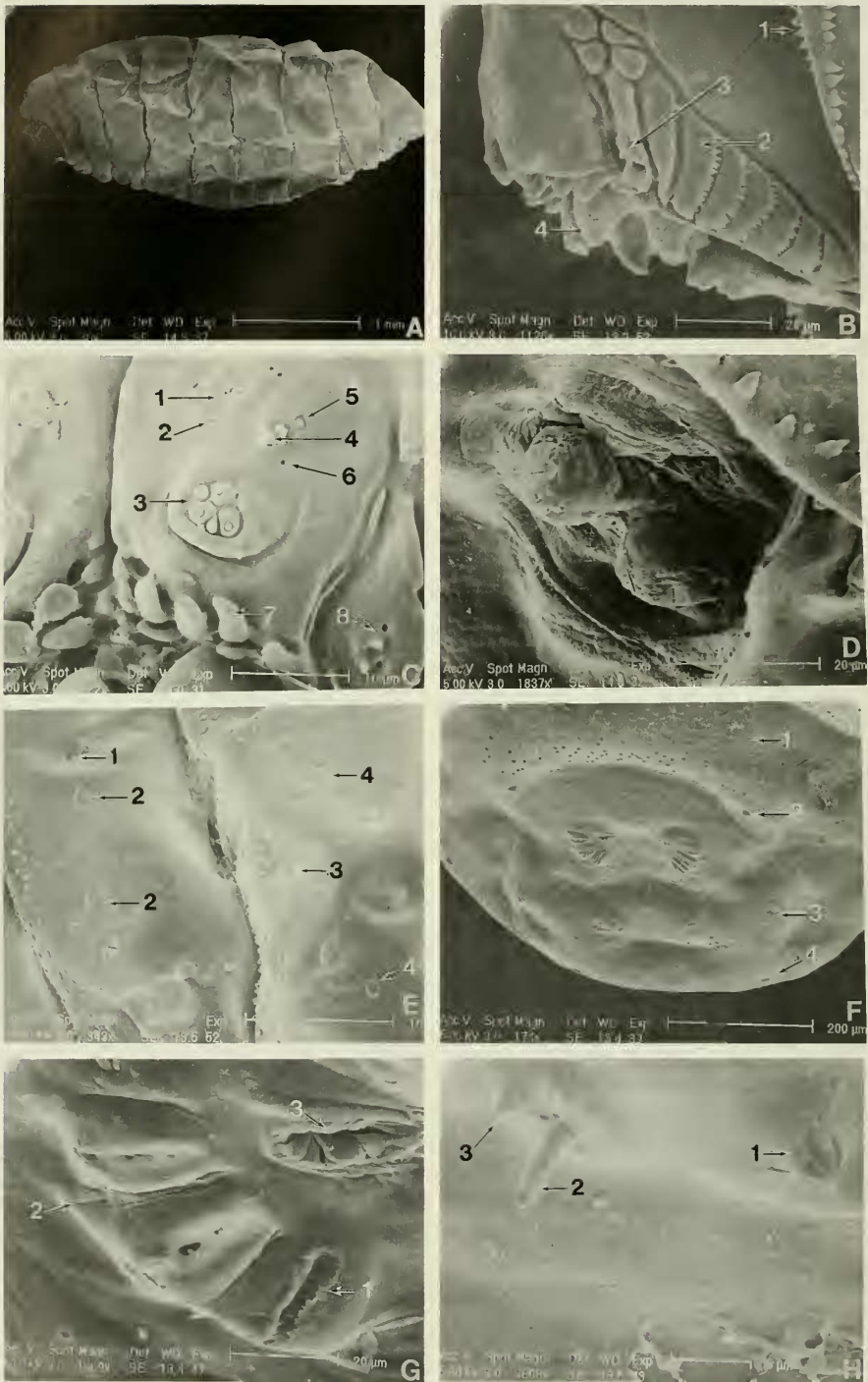


Fig. 2. Third instar of *Neaspilota pubescens*: (A) habitus, anterior to left; (B) gnathocephalon, lateral view, 1-minute acanthae, 2-oral ridge, 3-stomal sense organ, 4-mouthhook; (C) anterior sensory lobe, 1-dorsal sensory organ, 2-pore sensillum, 3-terminal sensory organ, 4-lateral sensory organ, 5-supralateral sensory organ, 6-pit sensory organ, 7-integumental petal, 8-stomal sense organ; (D) anterior thoracic spiracle; (E) metathoracic (left) and abdominal (right) lateral spiracular complexes, 1-spiracle, 2-verruciform sensilla on metathorax,

sory organ (Fig. 2C-5), and pit sensory organ (Fig. 2C-6); eight, papilliform (above) or spatulate (below), integumental petals in two rows above each mouthhook (Fig. 2C-7); eight oral ridges (Fig. 2B-2), all but most ventral ridge, toothed ventrally and lateral to oral cavity; stomal sense organ (Figs. 2B-3, C-8) ventrolaterad of anterior sensory lobe; mouthhook (Fig. 2B-4) tridentate (not shown); median oral lobe laterally flattened, apically pointed (not shown); prothorax circumscribed by minute acanthae (Fig. 2B-1); verruciform sensilla circumscribe prothorax posteriorad of minute acanthae (not shown); anterior thoracic spiracle on posterior margin of prothorax bears two oblong papillae (Fig. 2D); meta-thoracic lateral spiracular complex with a spiracle (Fig. 2E-1) and three verruciform sensillae, one above (not shown) and two below the spiracle (Fig. 2E-2); abdominal lateral spiracular complex with a spiracle (Fig. 2E-3) and two verruciform sensilla (Fig. 2E-4) dorsoposteriorad of, and two verruciform sensilla ventroposteriorad of, the spiracle, these sensilla arranged as two vertical pairs; caudal segment circumscribed dorsally by minute acanthae (Fig. 2F-1); a stelex sensillum dorsolaterad (Fig. 2F-2), laterad (Fig. 2F-3), and ventrolaterad (Fig. 2F-4) of posterior spiracular plate (Fig. 2G); each posterior spiracular plate (Fig. 2G) bears three ovoid rimae (Fig. 2G-1), ca. 0.03 mm in length, and four interspiracular processes (Fig. 2G-2), each with one to three, simple, pointed or forked branches, longest branch measuring 0.013 mm; intermediate sensory complex (Fig. 2H) with a medusoid sensillum (Fig. 2H-1) and a stelex sensillum (Fig. 2H-2). Each stelex sensillum surrounding the posterior spiracular plate apparently has a single,

hemispherical, minute acanthus at its base (Fig. 2H-3).

The habitus of the third instar of *N. pubescens* generally is like that reported for *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c). Like *N. signifera* (Goeden 2000a) and *N. appendiculata* (Goeden 2000c), only the anterior part of each body segment of *N. pubescens* is circumscribed by minute acanthae, whereas, in *N. aenigma* the anteriors, pleura, and posteriors of each segment are thus circumscribed (Goeden 2000b); in *N. wilsoni*, all intersegmental areas and all abdominal segments except the pleura are circumscribed (Goeden and Headrick 1999); and in *N. viridescens*, the intersegmental areas are free of acanthae (Goeden and Headrick 1992). Like *N. viridescens* (Goeden and Headrick 1992) and *N. wilsoni* (Goeden and Headrick 1999), but not like *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b) and *N. appendiculata* (Goeden 2000c), the dorsal sensory organ is not well defined, and flattened, and not dome-shaped, in the third instar of *N. pubescens* (Fig. 2C-1). In the second instar of *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. appendiculata* (Goeden 2000c), and *N. pubescens* (Fig. 1C-1) the dorsal sensory organ is both prominent and dome-shaped, as it is in the first instar of all congeners except *N. signifera*, where it was hidden in my specimens and could not be examined for comparison (Goeden 2000a), and in the present study where first instars were not available.

Additional similarities involved the integumental petals in the third instars of all

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3-spiracle, 4-verruciform sensilla on first abdominal segment; (F) anal segment, 1-minute acanthae, 2-dorsolateral stelex sensillum, 3-lateral stelex sensillum, 4-ventrolaterad stelex sensillum; (G) posterior spiracular plate, 1-rima, 2-interspiracular process, 3-ecdysial scar; (H) intermediate sensory complex, 1-medusoid sensillum, 2-stelex sensillum, 3-basal, conical, minute acanthus.

five congeners examined to date, all of which are papilliform and arranged in a double row above each mouthhook (Goeden and Headrick 1992, 1999; Goeden 2000a, b, c). The stomal sense organ of the third instar of *N. pubescens* bears one or two verruciform sensilla, two pore sensilla, and one or two, cone-shaped or short papilliform sensilla (Fig. 2C-8). Thus, it appears similar in complexity to the stomal sense organ of the second instar (Figs. 1B-3, C-6); however, the stomal sense organs of the third instars of four congeneric species appear especially well-developed compared to earlier instars and each bears different combinations of sensory structures, variously described as several cone-shaped sensilla in *N. viridescens* (Goeden and Headrick 1992); as papilliform and pit-type in *N. wilsoni* (Goeden and Headrick 1999); as verruciform or "compound verruciform" in *N. signifera* (Goeden 2000a), and verruciform and pit-type in *N. aenigma* (Goeden 2000b).

The third instars of all six species of *Neaspilota* examined to date have oral ridges with dentate ventral margins characteristically arranged in vertical series ventrolaterad of the dorsal sensory organ and laterad of the oral cavity. Similar oral ridges also were described in the second instars of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), and *N. appendiculata* (Goeden 2000c). The oral ridges number eight in *N. pubescens* (Fig. 2B-2), seven or eight in the third instar of *N. aenigma* (Goeden 2000b), seven in *N. appendiculata* (Goeden 2000c), but six in the second and third instars of the other three congeners examined to date. The appearance and arrangement of these oral ridges appears to be a generic character; however, the present study and Goeden (2000c) confirm that the oral ridges vary in number among third instars of *Neaspilota* species. Also, the most ventral, eighth oral ridge of *N. pubescens* is not ventrally toothed (Fig. 2B-2). The third instars of

Trupanea imperfecta (Coquillett), *T. jonesi* Curran, *T. nigricornis* (Coquillett), *T. pseudovicina* (Hering), *T. signata* Foote, and *T. wheeleri* Curran also bear serrated oral ridges (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al. 1998; Knio et al. 1996; Teerink and Goeden 1999), but these oral ridges appear to be fewer in number, and are not arranged in a more or less regular, vertical row lateral to the mouth hook, as in *Neaspilota*.

The mouthhooks of the third instars of *N. appendiculata*, *N. aenigma*, *N. signifera*, *N. viridescens*, and probably *N. pubescens* (unpublished data), are tridentate (Goeden and Headrick 1992; Goeden 2000a, b); whereas, those of the third instar of *N. wilsoni* are bidentate (Goeden and Headrick 1999). Such interspecific differences in dentation are supported by our findings that the mouthhooks of third-instar *Trupanea vicina* are bidentate; whereas, those of 12 other congeners examined from California are tridentate (Goeden and Teerink 2000b and citations therein).

The number and appearance of the stelex sensilla surrounding the posterior spiracular plate differ among the *Neaspilota* species examined to date. These number only four in the first instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000), but, unfortunately, were not observed with *N. signifera* (Goeden 2000a) or in the present study. This count of stelex sensilla remains at four in the second instars of *N. aenigma* (Goeden 2000b), *N. appendiculata* (Goeden 2000c), and *N. pubescens*, increases to six in third instars of *N. wilsoni* (Goeden and Headrick 1999), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c). These stelex sensilla also show inter-instar (intraspecific) and interspecific differences in the incidence and appearance of the minute acanthae that may ring them basally, but this was not recognized, studied or recorded by my coworkers and me until recently (Goeden 2000b, c; Fig. 2H-2, -3).



Fig. 3. Puparium of *Neaspilota pubescens*: (A) habitus, anterior to left; (B) anterior end, 1—invagination scar, 2—anterior thoracic spiracle; (C) caudal segment, 1—rima, 2—interspiracular process, 3—intermediate sensory complex.

Puparium: Mostly pale yellow, with posterior two-three segments grayish to blackened posteriorly, ellipsoidal, and smoothly rounded at both ends (Fig. 3A); anterior end

bears the invagination scar (Fig. 3B-1) and anterior thoracic spiracles (Fig. 3B-2); caudal segment circumscribed by minute acanthae; three stalex sensilla, dorsolaterad, lateral, and ventrolateral of posterior spiracular plates; posterior spiracular plate bears three broadly elliptical rimae (Fig. 3C-1), and four interspiracular processes, each with one to three branches (Fig. 3C-2); intermediate sensory complex (Fig. 3C-3) with a medusoid sensillum and a stalex sensillum. Seven puparia averaged 2.79 ± 0.05 (range, 2.55–2.95) mm in length; 1.31 ± 0.06 (range, 1.10–1.60) mm in width.

DISTRIBUTION AND HOSTS

Freidberg and Mathis (1986) described the distribution of *N. pubescens* as "Southern California south of 35° north latitude and west of the Sierra Nevada Mountains." Freidberg and Mathis (1986) and Foote et al. (1993) mapped the distribution to include only California.

The only reported and confirmed host plant of *N. pubescens* (reported as *appendiculata*) is *Lessingia* (reported as *Corethrogyne*) *filaginifolia* by Goeden (1989), which belongs to the subtribe Solidagininae of the tribe Astereae in the family Asteraceae (Hickman 1993, Bremer 1994). This perennial subshrub has at least two distinct varieties and itself is widely distributed in coastal scrub, oak woodlands, and grassland below 2,600 m throughout California and into adjacent southwestern Oregon and northern Baja California, Mexico (Hickman 1993, Shreve and Wiggins 1964), where *N. pubescens* also probably occurs.

Host records in Freidberg and Mathis (1986) present a quandary, as only *N. brunneostigmata* Doane is reported from *Lessingia* (reported as *Corethrogyne*) *filaginifolia*, including both varieties *filaginifolia* and *californica* (deCandolle) M. A. Lane (reported as *C. californica*). Neither of these records obtained from Wasbauer (1972) had been checked by Freidberg and Mathis (1986). Instead, both varietal records probably should refer to *N. pubescens*, not *N.*

brunneostigmata. On the other hand, I have only reared *N. brunneostigmata* from *Lesingia glandulifera* A. Gray and *L. lemmonii* A. Gray, never *N. pubescens*, which is easily distinguished from the former tephritid using the keys in Freidberg and Mathis (1986) and Foote et al. (1993). The latter host record for *N. brunneostigmata* (as *aenigma*) was first reported by Goeden (1989), and was corrected in Foote et al. (1993). The host record for *L. glandulifera* is new. Both represent the only confirmed host records for *N. brunneostigmata*. The seven other host records for *N. brunneostigmata* listed by Wasbauer (1972) and repeated by Freidberg and Mathis (1986) remain unconfirmed and refer either to undocumented records or to probable misidentifications listed in Foote and Blanc (1963), which, of course, predated Freidberg and Mathis (1986). In summary, I believe that *N. pubescens* is a true monophage, and I suspect, the better plant taxonomist in the case whereby *C. filaginifolia* was renamed *L. filaginifolia* (Hickman 1993).

BIOLOGY

Egg.—In each of three, closed, preblossom, immature flower heads of *L. filaginifolia*, a single egg was inserted pedicel-last; two of these eggs had their long axes perpendicular to the receptacle, one rested at a 45° angle to the receptacle. The last egg had been inserted through the phyllaries and was embedded for half its length in the corolla of a peripheral floret; whereas, the other two eggs were placed between an inner phyllary and a peripheral floret. The diameters of the receptacles of these flower heads containing eggs averaged 1.7 ± 0.17 (range, 1.40–1.99) mm.

Larva.—Upon eclosion, the only two first instars found feeding in separate, preblossom flower heads either tunneled into an ovule, or into a corolla before entering the ovule to which the corolla was basally attached. The receptacles averaged 1.4 mm in diameter and an average of 1.5 ovules

was damaged in these two flower heads. Neither receptacle was abraded or pitted by feeding.

Second instars continued feeding on ovules in preblossom flower heads or on soft achenes in open, blossom and post blossom flower heads. All fed within a series of adjacent ovules/soft achenes with their bodies more or less perpendicular to and their mouthparts directed towards the receptacles, but always above the receptacles. Receptacles of 12 flower heads containing second instars averaged 1.92 ± 0.17 (range, 1.42–3.42) mm in diameter. These flower heads each contained a single larva that had destroyed an average of 3.8 ± 0.6 (range, 1–8) ovules/soft achenes. Based on 23 (range, 17–34) as the average total number of ovules and achenes respectively counted in 40 preblossom to postblossom flower heads, about 9.5% (range, 2.5–20%) of the ovules/soft achenes in the 12 flower heads were damaged by second instars.

Third instars (Fig. 4A) initially continued to feed mainly on soft achenes in blossom or postblossom flower heads. Twenty-four flower heads that averaged 1.95 ± 0.14 (range, 1.10–2.56) mm in diameter each contained a single third instar. An average of 15 ± 2.1 (range, 4–34) of the soft achenes therein were damaged, or about 38% (range, 10–100%) of the average total of 40 ovules/soft achenes per flower head. These percentages of seed predation per larva per flower head, like those reported for *N. aenigma* (Goeden 2000b) and *N. appendiculata* (Goeden 2000c), are on the high side among florivorous tephritids studied by us to date (Headrick and Goeden 1998). This percent seed destruction per flower head is exceeded only by gregarious florivorous species like *Trupanea conjuncta* (Adams) (Goeden 1987) and *T. pseudovicina* Hering (Goeden and Teerink 1998) or by species with large larvae that develop in immature or small flower heads like *Paracantha cultaris* (Coquillett) (Cavender and Goeden 1982) and *Xenochaeta dichromata* Snow (Goeden and Teerink 1997a). Also, it

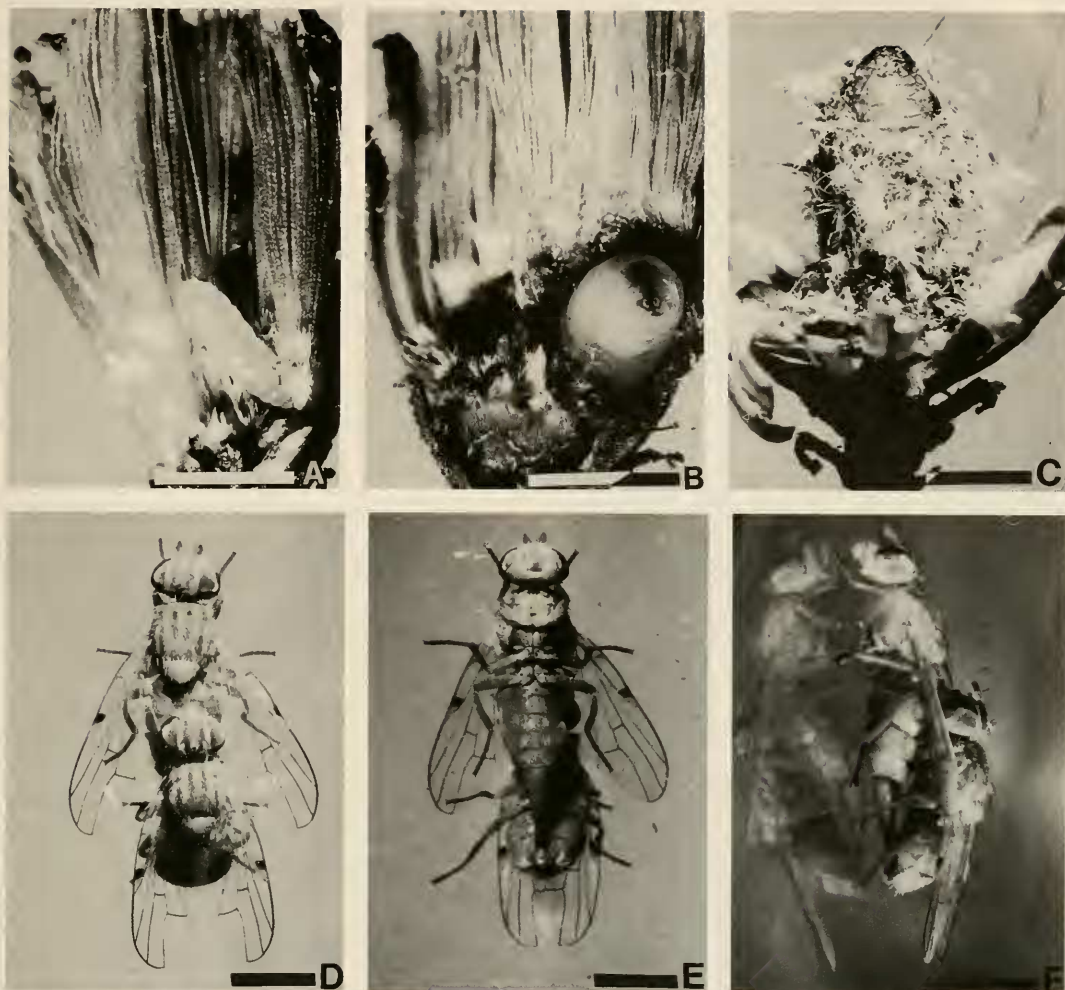


Fig. 4. Life stages of *Neaspilota pubescens* in *Lessingia filaginifolia*: (A) early third instar feeding on soft achenes in open flower head, (B) late third instar feeding on soft achenes in open flower head, (C) puparium formed in spring by overwintered prepuparium in flower head, (D) mating adults, dorsal view, (E) mating adults, ventral view, (F) mating adults lateral view. Lines = 1 mm.

should be noted that the rates of flower head infestation per sample for *N. pubescens* was very low, e.g., mean of 4.5% (range, 1.5%–10%) for five samples, like most *Neaspilota* in nature that we have studied (unpublished data).

Third instars in flower heads fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 4B). Only five (21%) of the third instars in the 24 infested heads scored or pitted the receptacles; however, most presumably supplemented their diet with

sap. Goeden and Headrick (1992, 1999) and Goeden (2000c) described and discussed this similar type of feeding by *N. viridescens*, *N. wilsoni*, and *N. appendiculata*, respectively. And, as also reported for all three of these congeners that overwinter as prepuparia (Goeden and Headrick 1992, 1999; Goeden 2000c), most third instars became surrounded for about 90% of their lengths by cells, which occupied most of the interior of the flower heads and consisted of ovule-, achene-, chaff-, pappus-, and corolla-fragments cemented together by

liquid feces and sap that hardened when dry (Fig. 4C). These protective cells were slightly larger than the mature larvae, externally incorporated the outer walls of achenes and the few uneaten achenes, and were blackened and smooth inside (Fig. 4C). Upon completing feeding and cell construction, the larvae oriented with their anterior ends towards the receptacles, retracted their mouthparts, and formed prepuparia (Headrick and Goeden 1998). Most individuals overwintered in diapause as prepuparia (Goeden and Headrick 1992, 1999; Goeden 2000c; Headrick and Goeden 1998), but a few individuals pupariated early and emerged in summer (July–August). Prior to pupariation the prepuparia reversed their orientation within their cells and turned 180° such that their heads were directed away from the receptacles (Fig. 4C).

Adult.—Adults emerged from overwintered, mature flower heads, and probably are long-lived. Under insectary conditions, five unmated males averaged 67 ± 23 (range, 23–152) days, but only two virgin females were available for study and averaged 27 (range, 24–30) days. Such lengthy longevities for males compare favorably with average adult longevities reported for adults of *N. viridescens* (Goeden and Headrick 1992), *N. wilsoni* (Goeden and Headrick 1999), *N. signifera* (Goeden 2000a), *N. aenigma* (Goeden 2000b), and *N. appendiculata* (Goeden 2000c).

The pre mating and mating behaviors of *N. pubescens* were not studied in the field, but were observed in petri dish arenas found to be so useful with many other non-congeneric, nonfrugivorous, tephritid species (Headrick and Goeden 1994). Premating behaviors observed with paired *N. pubescens* were abdominal pleural distension and side-stepping by males while tracking females (Headrick and Goeden 1994) and rapid wing hamation, sometimes combined with lofting about 20° by both sexes (Headrick and Goeden 1994). No trophallaxis or nuptial gift presentation was noted as reported with *N. viridescens* (Goeden and

Headrick 1992). Seven matings, six by one pair during a 2-week period (Figs. 4D, E, F) were observed that began during late afternoon at dusk and lasted an average of $1,032 \pm 73$ (range, 850–1,440) min (or 17 h and 12 min on average). This was three to five times longer than the average durations of 190 min reported for *N. aenigma* (Goeden 2000b), 235 min reported for *N. wilsoni* (Goeden and Headrick 1999), 238 min reported for *N. signifera* (Goeden 2000a), 285 min reported for *N. appendiculata* (Goeden 2000c), and 318 min reported for *N. viridescens* (Goeden and Headrick 1992). It also was among the longest mating durations reported by my collaborators and me (Headrick and Goeden 1994), exceeded only by a pair of *Tephritis baccharis* (Coquillett) that mated for 2 days and nights under similar conditions (Goeden and Headrick 1991). A pair of *Dioxya picciola* (Bigot) was reported to stay together in the field for 28 h, during which time they copulated and oviposited three times in one day, remained *in copula* on one flower head overnight, and copulated and oviposited again three times during the following day (Headrick et al. 1996), but this involved mate guarding (Headrick and Goeden 1994, Headrick et al. 1996), also observed with *N. signifera* (Goeden 2000a). As far as could be determined, the extended mating by *N. pubescens* involved continuous copulation.

The only precopulatory behavior observed for the female was an elevation of the oviscape 20° to 30° coupled with rapid wing hamation and lofting, which may have signaled receptivity (but see postcopulatory behavior below). A male was observed to initiate mating by rapidly pursuing and grabbing the head of the female from the front with his forelegs and -tarsi, and wrestling her into submission while he mounted her. No copulatory induction behavior was noted with *N. pubescens* and intromission was gained rapidly. Most matings were observed only after copulation had begun, suggesting that precopulatory behavior was

perfunctory. The mating position (Figs. 4D, E, F) was such that the wings of the male were parted about 20° , while the wings of the female were parted at about 60° , with both pairs of wings centered over their respective body midlines (Figs. 4D, E). The body of the female was parallel to the substrate, while the body of the male was elevated about 20° anteriorly (Fig. 4F). The hind- and midtarsi of the male usually rested on the substrate, but sometimes his midtarsi grasped the base of the ovipositor, while his foretarsi hooked onto the abdominal pleura of the female midway along the abdomen (Figs. 4D, F). The male's mouthparts were positioned above the second abdominal tergite of the female (Figs. 4D, F). In this position the male tenaciously held onto the female as copulation continued, while defeating her increasingly vigorous efforts to dislodge him. These dislodgment efforts by the female consisted of walking rapidly, then stopping to strongly arch her dorsum at the juncture of her thorax and abdomen while rapidly hamating and lofting her wings (Fig. 5A), or bending her ovipositor upward, while kicking at his head, ventrum, and mid- and hind legs with her hind legs and tarsi. In between these bouts of female "restlessness," the pair largely remained quiescent with only their mouthparts pumping, or sometimes both forming regurgitation droplets (Headrick and Goeden 1994), or while the female groomed her head and fore legs. Besides tightly clinging to the female, the male sometimes repositioned his foretarsi so as to gain better purchase or rub his midtarsi alternately along her ovipositor to induce passivity as a variation on copulatory induction behavior (Headrick and Goeden 1994). These bursts of activity by the female always preceded disengagement, but only infrequently resulted in disengagement. What action(s) finally triggered or caused the pair to separate, remain unanswered.

Two mating terminations and disengagements were observed, which involved each male turning in place and walking away

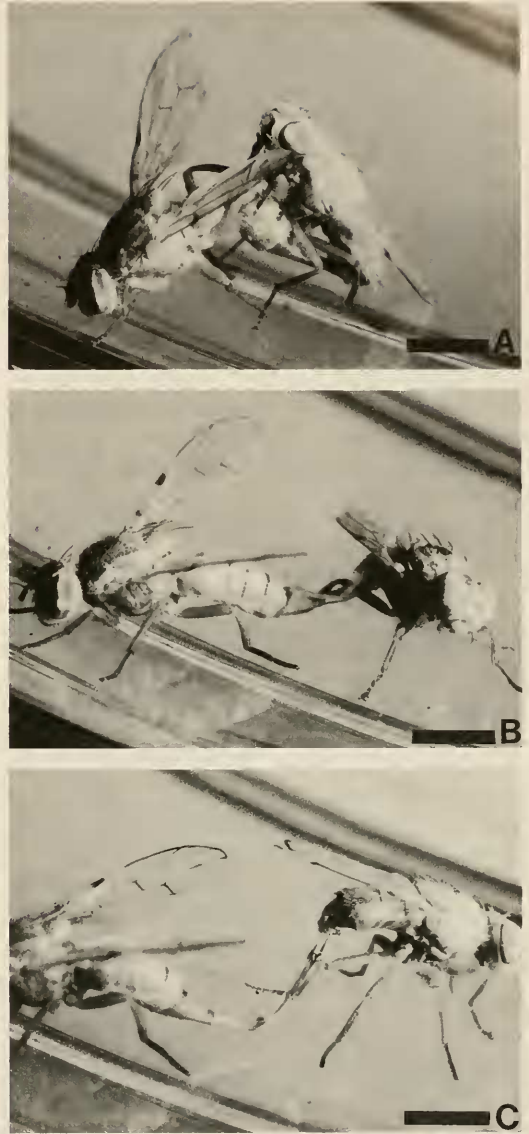


Fig. 5. Disengagement sequence at termination of mating by *Neaspilota pubescens*: (A) female arching dorsum and kicking at male with hind legs and tarsi, (B) male turning and stepping off female, (C) male pulling genitalia from female as he walks away. Lines = 1 mm.

from the female while pulling his genitalia from within her, a process that lasted less than 10 s in both cases (Figs. 5A, B, C). Postcopulatory behavior by *N. pubescens* mainly consisted of storing of the genitalia by males and cleaning and grooming by both sexes (Headrick and Goeden 1994); al-

though, instances of a female strongly elevating her oviscapae was seen, as she ran away from a pursuing male to avoid recoupling following disengagement. As noted above, this same behavior often preceded mating.

Seasonal history.—The life cycle of *N. pubescens* in southern California follows an aggregative pattern (Headrick and Goeden 1994, 1998) in which the prepuparium is the principal overwintering stage. Come late spring (May), overwintered prepuparia reverse their orientation in their cells in flower heads on shoots of dead host plants and pupariate. Adults emerge during late May and early June and aggregate on preblossom shoots of *L. filaginifolia* to mate. Females oviposit in the small, newly formed, closed, preblossom flower heads in July and larvae feed until fully grown, then enter diapause in early fall (September–October). There is a single generation per year on their sole host plant, although as mentioned above, a few adults emerge in late August–September, perhaps to produce a partial generation on late-flowering plants, or to overwinter as long-lived adults.

Natural enemies.—A single female of *Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from a puparium of *N. pubescens* as a solitary, larval-pupal endoparasitoid.

ACKNOWLEDGMENTS

I thank Andrew C. Sanders, Curator of the Herbarium, Department of Botany and Plant Sciences, University of California, Riverside, for identifications of plants mentioned in this paper. Krassimer Bozhilov in the Institute of Geophysics and Planetary Physics, University of California, Riverside, greatly facilitated my scanning electron microscopy. The parasitoid was identified by Harry E. Andersen, Huntington Beach, California. I also am grateful to Jeff Teerink and Kristine Gilbert for technical assistance and to Louie Blanc, David Headrick, and Jeff Teerink for their helpful comments on earlier drafts of this paper.

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